Subterranean Biology 55: 95–108 (2026)
doi: 10.3897/subtbiol.55.186321
https://subtbiol.pensoft.net

SHORT COMMUNICATION

A peer-reviewed open-access journal
Subterranean Biology
Published by The International Society for Subterranean Biology

Subterranean temnocephalid flatworms of the Dinaric Karst are not picky about the hosts but compete for them: an analysis of literature data

Cene Fišer[1], Ester Premate[1], Valerija Zakšek[1]

1 *SubBioLab, Department of Biology, Biotechnical Faculty, University of Ljubljana, Jamnikarjeva 101, Ljubljana, Slovenia*

Corresponding author: Valerija Zakšek (valerija.zaksek@bf.uni-lj.si)

Academic editor: Piter Boll | Received 25 January 2026 | Accepted 18 February 2026 | Published 9 March 2026

https://zoobank.org/7856C744-5BD5-45C1-A447-4ECF3B44A34E

Citation: Fišer C, Premate E, Zakšek V (2026) Subterranean temnocephalid flatworms of the Dinaric Karst are not picky about the hosts but compete for them: an analysis of literature data. Subterranean Biology 55: 95–108. https://doi.org/10.3897/subtbiol.55.186321

Abstract

Epizoic-host species interactions in subterranean environments are rare and poorly understood. A little-known case of epizoic-host interaction involves flatworms (Temnocephalidae) and large subterranean crustaceans (cave shrimps of the family Atyidae and amphipods of the genus *Niphargus*) living along the Dinaric Karst. The taxonomy and distribution of Dinaric temnocephalids were thoroughly studied in the previous century. There are 15 subterranean temnocephalid species living on different crustacean species in the area. However, analyses of associations between epizoic and host species, as well as co-occurrence of epizoic species, are lacking. In this study, we extracted literature data and analysed epizoic-host interactions using network analysis, complemented by co-occurrence patterns among temnocephalid species. The network analysis indicates low host specificity between temnocephalids and crustaceans; one species is specialized on *Niphargus*, whereas the others attach to different cave shrimp species. Of these, only one species seems to be specialized to a specific host body part, while the rest can attach to different body parts of cave shrimps. The analysis of co-occurrence patterns implies that many temnocephalid species pairs generally compete for their hosts. We conclude that epizoic-host specificity in subterranean temnocephalids, detectable at the order level, evolved long ago, and that most species cannot be highly specialized due to oligotrophic conditions in caves. As a result, there is substantial competition among them for a host. We discuss potential caveats of the study based solely on the literature and provide a roadmap for future research.

Keywords

Atyidae, epizoic-host interactions, interspecific competition, *Niphargus*, Platyhelmithes, Temnocephalidae, temnocephalid-crustacean interaction

Copyright *Cene Fišer et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Interspecific interactions contribute to many biodiversity-generating processes, such as community assembly (Vellend 2010), adaptive evolution (Schluter 2000; Stuart and Losos 2013) and speciation (Brodersen et al. 2018; Medina et al. 2022). The contribution of interspecific interactions to biodiversity-generating processes can be best studied in relatively simple communities comprising few species and little environmental heterogeneity, such as communities from subterranean environments (Mammola 2019). The potential of subterranean communities for studying interspecific interactions, however, remains underexplored. Most of our knowledge about interactions among subterranean species comes from comparative studies. Some interactions received much attention, whereas others are hardly mentioned. One of the most studied interactions, interspecific competition, was invoked as a plausible explanation for patterns of character displacement (Fišer et al. 2015a; Delić et al. 2016), ecological niche differentiation (Trontelj et al. 2012; Mammola and Isaia 2014; Mammola et al. 2020; Pavlek and Mammola 2020) and spatial distribution of species pairs (Fišer et al. 2015b, 2019; Delić et al. 2025). Predation was assessed less frequently, mainly focusing on how predation relates to the evolution of trophic morphology and defence structures (Jugovic et al. 2010; Hutchins et al. 2014; Premate et al. 2021a, 2021b). Little is known about parasitism (Weigand et al. 2016; Amin et al. 2019; Benko et al. 2024). Neglected yet interesting are epizoic interactions between temnocephalid flatworms and subterranean crustaceans, well documented in taxonomic studies and monography, but not assessed within the ecological framework (Matjašič 1956, 1990; Gelder 1999).

Temnocephalidae are a family of freshwater epizoic flatworms (Rhabdocoela, Platyhelminthes), found in all habitable continents except for Africa and North America (Blair et al. 2023). They most commonly attach to freshwater crustaceans, but also to other invertebrates and, more rarely, to vertebrates, e.g., turtles. Temnocephalids are highly specialized for an epizoic way of life, mostly lacking locomotory cilia, but having anterior tentacles and a posterior sucker-like attachment organ (Blair et al. 2023). In the Dinaric Karst (Balkan Peninsula), temnocephalids were intensively studied from the 1960s to the 1990s by the late Professor Janez Matjašič, who documented their taxonomy, distribution, host identities, and preferred attachment site on host bodies (Matjašič 1990). In his monograph, he reported 15 subterranean temnocephalid species from five genera, associated with multiple crustacean hosts (Matjašič 1990). The coexistence of numerous epizoans and multiple host species represents an interesting system for the study of twofold interactions: epizoan-host specificity and epizoan-epizoan competition for hosts.

In this study, we reviewed published data on temnocephalid flatworms living on subterranean crustaceans of the Dinaric Karst and analysed them within the ecological framework. Within this pilot study, we addressed two main questions. First, we investigated epizoan–host interactions to assess the level of host specificity in temnocephalids. The analysis was performed at three hierarchical levels: at the level of temnocephalid genera and currently valid cave shrimp genera (Jugovic et al. 2026), at the species level (for both epizoans and hosts) and at the host body part level. Second, we questioned

whether different temnocephalid species compete for their hosts. Hence, we analysed co-occurrences among different commensals, while considering their geographic origin, host species and the temphocephalid preferred attachment site on the host's body. Finally, we critically reviewed the results and limitations of our literature-based approach and provided a roadmap for future research on epizoic interactions in subterranean environments.

Materials and methods

The data on temnocephalid species were acquired from the literature (Matjašič 1990; Gelder 1999). For each record, we extracted information on the species, the cave (locality) where each species was found, and the host and body part to which each species attaches. In the case of amphipod hosts (genus *Niphargus*), several species names are most likely outdated (see Fišer and Premate 2024; Premate and Fišer 2024). Given that not all names can be inferred from the locality only, we retained them in their original form, but in the analyses, we treated them at the genus level (*Niphargus*). The shrimp species was revised using shrimp taxonomy, phylogeny and distribution, acquired from the recent publication (Jugovic et al. 2026) (Fig. 1).

We studied epizoic-host interactions using a bipartite network approach (Dormann et al. 2009). We explored associations at two hierarchical levels (epizoan and host species and genera), resulting in four networks. The first included five temnocephalid genera and three host clades, namely the amphipod genus *Niphargus*, the shrimp clade *spelaeocaris* (comprising genera *Spelaeocaris* and *Troglocaridella*) and the shrimp clade *troglocaris* (comprising genus *Troglocaris*). The second included five temnocephalid genera and host body part occupancy. The third and fourth networks were more detailed: we analysed the association between temnocephalids and their host species, and between temnocephalid species and body-part occupancy, respectively.

To describe these relationships, we parametrized the networks using network-level and node-level metrics and tested for significance using null models. Null models provide a distribution of random networks and allow an estimation of whether the estimated parameter is exceptionally small or large. The interaction matrices (epizoan genera x host genera, epizoan species x host species, and epizoan species x host body part occupancy) were permuted 999 times, while preserving row and column totals. The association was labelled binary (0,1) as confirmed/non-confirmed. We compared the observed metrics to those derived from random networks using the function ses() from the R package BAT (Cardoso et al. 2024). P values were calculated using a nonparametric method due to asymmetry of the distributions of metrics derived from null models, except in one case (network-level metrics in the third network, i.e., epizoan and host species).

We assessed multiple network-level metrics (connectance, nestedness metric based on overlap and decreasing fill (NODF), H2', generality and vulnerability) using binary (0,1) interaction matrices. Connectance describes the proportion of realized pairwise interactions against all possible interactions. High connectance thus indicates many epizoan-host interactions relative to the network's size. Nestedness was quantified using

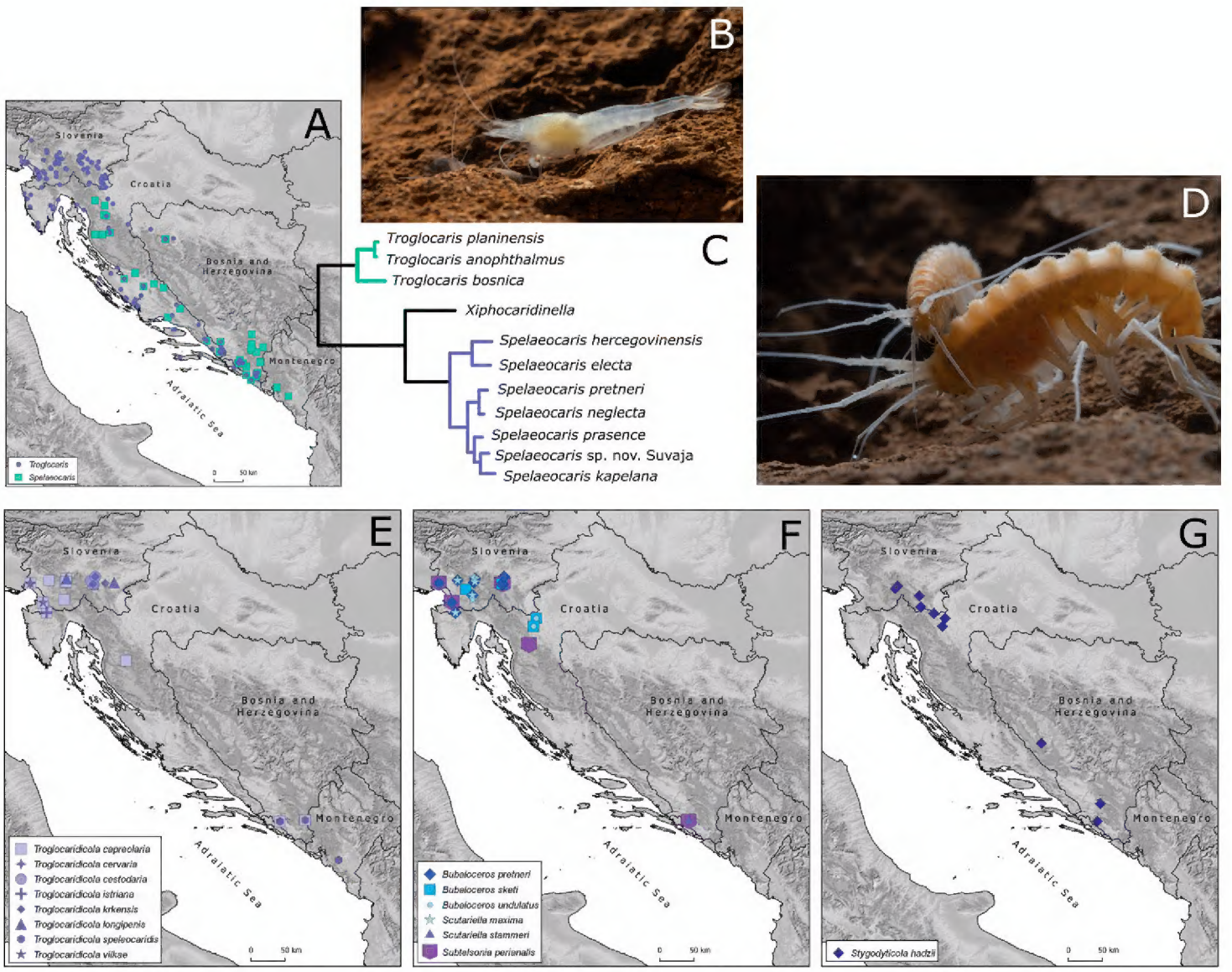

Figure 1. A Distribution of cave shrimps from the genera *Troglocaris* and *Spelaeocaris* and temnocephalid genera and species (**E, F, G**) along the Dinaric Karst. **C** Phylogenetic relationships of cave shrimp genera from the Dinaric Karst and Caucasus, simplified after Jugovic et al. (2026). Temnocephalid species from the genera *Troglocaridicola*, *Bubaloceros*, *Scutariella* and *Subtelsonia* (**E, F**) are epibionts on cave shrimps, while *Stygodyticola hadzii* (**G**) lives on amphipods from the genus *Niphargus*, which are common inhabitants in caves along the Dinaric Karst. Photographs of subterranean crustacean hosts, the cave shrimp *Spelaeocaris electa* (**B**, photo credit: Teo Delić) and the amphipod *Niphargus balcanicus* (**D**, photo credit: Teo Delić).

the NODF (Almeida-Neto et al. 2008), which assesses whether interactions of less connected species (specialists) are subsets of those of more connected species (generalists). High NODF describes a hierarchical structure in which specialists associate with hosts that are also used by generalist epizoans. H2' describes network-level specialization, i.e., how strongly interactions deviate from random expectations given marginal totals. Values close to 0 indicate generalized networks, whereas values close to 1 indicate specialized networks. Generality is calculated as the mean effective number of epizoan species per host (or body part); high generality indicates that hosts tend to carry more epizoans, whereas low generality indicates host-specificity. By contrast, vulnerability indicates the mean effective number of hosts (or body parts) per epizoan. A high vulnerability index indicates that epizoans are broadly distributed across their hosts, whereas a low index indicates host-specific epizoans.

In node-level metrics (degree and d'), the node equals the species in a network. We estimated node degrees, i.e., the number of interactions per node. Epizoan degree refers to the number of hosts occupied by epizoan species. A related d' describes node-level specialization; values close to 0 indicate generalists, whereas values close to 1 imply specialist genera or species.

We analysed the co-occurrence of different epizoan species at the cave, host, and host body part levels. A finer scale analysis was not possible due to the limited amount of data. This analysis was run using the model co-occur (Veech 2013, Griffith et al. 2016), which infers the association between two species from the frequencies of co-occurrences against the null expectation of random co-occurrences, i.e., more frequent, less frequent or as frequent as expected from randomly generated co-occurrences, while accounting for the number of records and commonness of the species. This analysis assumes unlimited dispersal within the study region.

We carried out the analyses in R 4.4.1 (R Development Core Team 2024), using packages cooccur 3.1 (Griffith et al. 2016), bipartite 2.23 (Dormann et al. 2009), and BAT 2.9.6 (Cardoso et al. 2024) for data analysis. Other packages used for data handling and visualization are listed in the R code available at Zenodo at https://doi.org/10.5281/zenodo.18355834.

Results

Temnocephalids are found along the entire Dinaric Karst (Fig. 1). The analyses of all networks imply that host-epizoan interactions are not specialized, regardless of the hierarchic level of analysis (Tables 1, 2, Fig. 2). Network-level metrics in "epizoan genus–host genus" did not deviate from random expectation, while the same metrics applied to "epizoan species–host species" indicated higher level of generalism than expected by chance. Notably, the amount of data was insufficient to estimate network-level metrics for "epizoan genus–host body part" occupancy and "epizoan species–host body part occupancy" (Table 1). Overall, we detected only one potentially specialist relationship using node-level metrics (Table 2). The species *Stygodyticola hadzii* is specialized for the genus *Niphargus* ("epizoan species – host species" analysis: d' = 1, p = 0.009). Moreover, the species *Subtelsonia perianalis* apparently preferentially occupies the shrimp's anus ("epizoan species–host body part occupancy" analysis marginally significant: d' = 1, p = 0.07, "epizoan genus–host body part occupancy" analysis not significant).

The results of co-occurrence analyses imply a modest level of competition (Fig. 3). On a locality level, most of the pairwise co-occurrences do not deviate from random expectation. *Stygodyticola hadzii* co-occurs with four other species less frequently than expected by chance. This species lives on the amphipod genus *Niphargus*; thus, the result likely reflects some other ecological dynamics, such as a preference for host species. The analysis at the host species level indicates that 21 temnocephalid pairs co-occur on the same host less frequently than expected by chance. The analysis at the level of host body

Table 1. Results of network-level metrics from bipartite network analyses. H2': network-level specialization. Connectance, nestedness (NODF) and H2' were evaluated using null models (999 random networks). Significant *P* values are in bold. All *P* values were calculated using nonparametric methods (except in the epizoan species–host species network). Generality describes the mean effective number of epizoans per host or host body part, and vulnerability describes the mean effective number of hosts or host body parts per epizoan. NA means that network metrics and null model evaluation were not possible due to data constraints.

Network metrics	Network			
	epizoan genera – host genera	**epizoan genera – host body part**	**epizoan species – host species**	**epizoan species – host body part**
Connectance	0.53	0.33	0.29	0.33
SES	0.96	0	2.96	0
P	0.34	1	**0.0031**	1
NODF	30.77	0	31.09	0
SES	-0.47	0	0.96	0
P	0.64	1	0.34	**1**
H2'	0	NA	0	NA
SES	-0.96	NA	-2.73	NA
P	0.37	NA	**0.0063**	NA
Generality	3.25	1.50	8.91	7.86
Vulnerability	1.75	1	1.91	1

parts implied that 23 species pairs occur in the same region of the host less frequently than expected by chance. Finally, many co-occurrences could not have been statistically evaluated due to the limited number of co-occurrences (empty cells in Fig. 3).

Discussion

In this study, we analysed an intriguing dataset describing the association between temnocephalid flatworms and their subterranean crustacean hosts. Despite the modest size of the dataset, we tentatively propose two conclusions and provide directions for further research.

Our first result indicates that temnocephalid host specificity is low and applies primarily to the order level (i.e., shrimp versus amphipod). If true, this pattern may suggest that obligate associations between epizoans and their hosts evolved long ago, at the onset of the formation of subterranean Dinaric fauna. A specialization of *Subtelsonia* for the perianal region of hosts seems to be the exception rather than the rule but may even reflect limitations in available data (see below). Overall, this view aligns with a hypothesis that groundwater communities are dominated by trophic generalists, as narrow specialization is unlikely to be sustainable in an oligotrophic environment (Gibert and Deharveng 2002). As epizoic life is a specialization *per se*, it seems plausible that further specialization is no longer sustainable in subterranean environments. On the other hand, preferential attachment to one body region in *Subtelsonia perianalis* could result from higher specialization on a food source, in this case, the intestinal content of

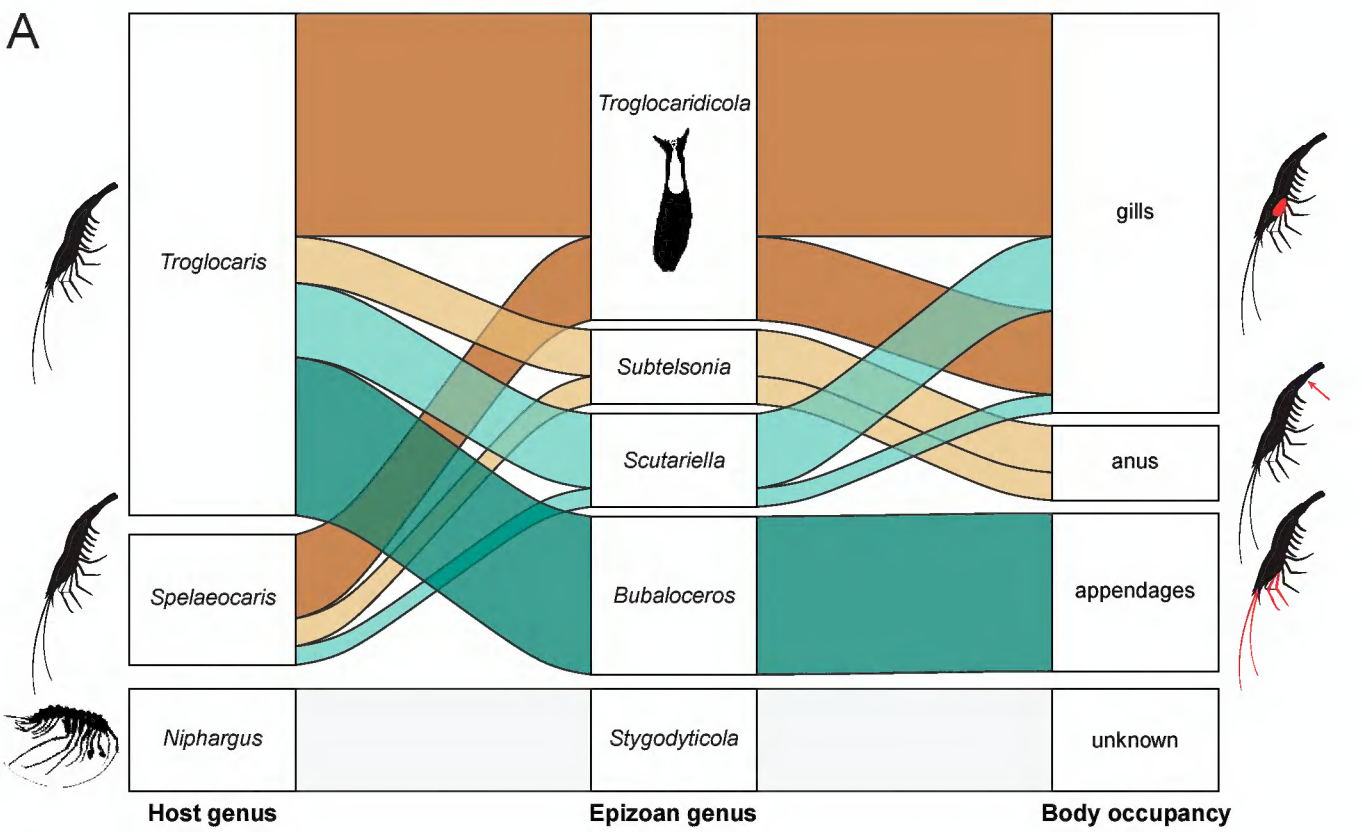

Figure 2. A Alluvial plot showing associations between hosts and epizoans (both on genus levels) and host body part occupancy (shown in red on silhouettes). *Spelaeocaris* includes the genera *Spelaeocaris* and *Troglocaridella* (see **B**) according to recent molecular phylogeny. **B, C** Bipartite networks of host species and epizoan species (**B**) and of epizoan species and host body part occupancy (**C**). Network metrics are available in Table 1. Epizoan genera *Troglocaridicola* abbreviated as *T.* and *Bubaloceros* as *B.* All panels: widths of the connections (edges) correspond to frequencies of associations, but no weights were used in network analyses (**B, C**). Different colours of the edges correspond to different epizoan genera.

Table 2. Results of node-level metrics from bipartite network analyses. deg.: degree (number of interactions per node), d': node-level specialization. Epizoan genera abbreviations: *B.*: *Bubaloceros*, *Sc.*: *Scutariella*, *St.*: *Stygodyticola*, *Su.*: *Subtelsonia*, *T.*: *Troglocaridicola.* d' evaluated using null models (999 random networks). Significant *P* values in bold. All *P* values calculated using nonparametric methods. NA is given where network metrics and null model evaluation were not possible due to data constraints. nr: not relevant in the given network.

Epizoan node	Network			
	Epizoan genera – host genera	**Epizoan genera – host body part**	**Epizoan species – host species**	**Epizoan species – host body part**
	deg./d'/SES/*P*	**deg./d'/SES/*P***	**deg./d'/SES/*P***	**deg./d'/SES/*P***
Bubaloceros	1/0/–0.67/0.50	1/1/0.67/0.50	nr	nr
B. pretneri	nr	nr	1/0/–0.49/0.63	1/0.52/0.93/0.35
B. sketi	nr	nr	1/0/–0.54/0.59	1/0.52/0.94/0.35
B. undulatus	nr	nr	1/0/–0.49/0.62	1/0.52/0.94/0.35
Scutariella	2/0/–0.80/0.42	1/0/–0.67/0.50	nr	nr
Sc. maxima	nr	nr	1/0/–0.56/0.58	1/0/–0.36/0.72
Sc. stammeri	nr	nr	3/0.016/–0.59/0.56	1/0/–0.35/0.73
St. hadzii	1/1/1.57/0.12	NA	2/1/2.61/**0.0089**	NA
Su. perianalis	2/0/–0.77/0.44	1/1/0.71/0.48	3/0.016/–0.65/0.52	1/1/1.79/0.07
Troglocaridicola	2/0/–0.76/0.45	1/0/–0.72/0.47	nr	nr
T. capreolaria	nr	nr	3/0.016/–0.66/0.52	1/0/–0.41/0.69
T. cervaria	nr	nr	1/0/–0.51/0.61	1/0/–0.41/0.69
T. cestodaria	nr	nr	1/0/–0.52/0.60	1/0/–0.36/0.72
T. istriana	nr	nr	1/0/–0.53/0.60	1/0/–0.35/0.73
T. krkensis	nr	nr	1/0/–0.55/0.58	1/0/–0.36/0.72
T. longipenis	nr	nr	1/0/–0.53/0.59	1/0/–0.37/0.71
T. speleocaridis	nr	nr	1/0.46/0.41/0.69	1/0/–0.35/0.73
T. vilkae	nr	nr	1/0/–0.57/0.57	1/0/–0.40/0.69

cave shrimps (Matjašič 1990). The lack of association between epizoan and host species implies that host speciation was not accompanied by epizoan coevolution. If so, this result suggests that extant temnocephalids can more effectively maintain gene flow among populations than their shrimp hosts can.

Our second result suggests that many co-occurrences of temnocephalids on a host species (or host body part) are lower than what would be expected by chance, which could indicate competitive interactions among epizoans (Griffith et al. 2016). Moreover, co-occurrences not deviating from random expectation could indicate either neutral population dynamics or an outcompetition-recolonization model of interaction between the epizoan species (Chesson 2000; Leibold and McPeek 2006). These conclusions are compatible with the results of our network analysis: if epizoans exhibit low host specificity, competitive interactions are not resolved through niche partitioning; therefore, epizoans must directly compete for the hosts and body parts to which they attach. We can further speculate that, in a highly competitive system, maintaining high mobility may be advantageous, as individuals displaced from a host must rapidly find and colonize another (alternative) host.

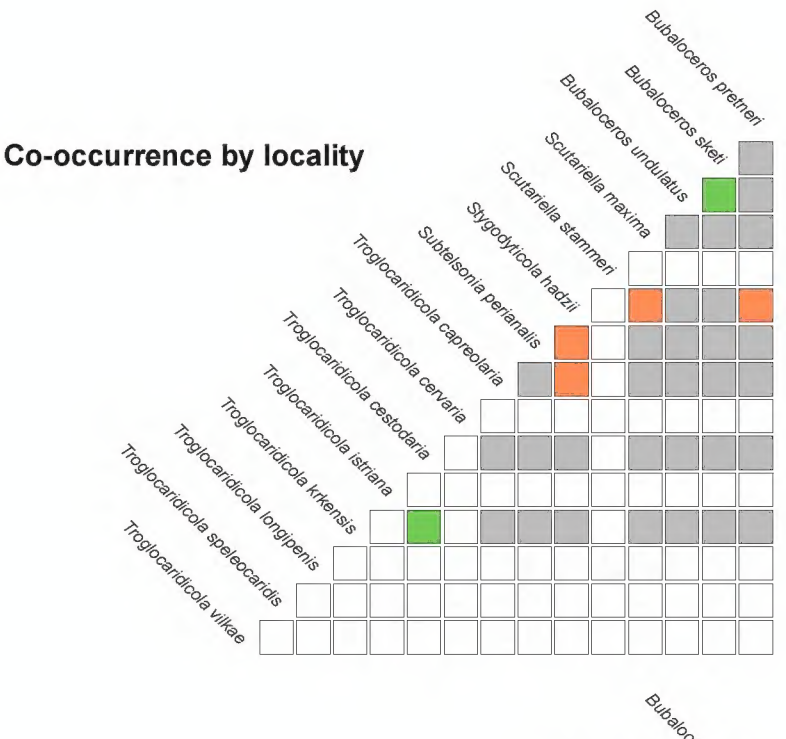

Figure 3. Results of the analysis of co-occurrence records by locality, host genus (*Spelaeocaris* including *Spelaeocaris* and *Troglocaridella*, *Troglocaris*, or *Niphargus*), and host body part (gills, anus, or appendages). Green and orange squares indicate, respectively, positive (species co-occur more often than expected by chance) and negative (species co-occur less often than expected by chance) species associations. Grey squares indicate random associations. In many cases, co-occurrence analysis was not possible due to data constraints (white squares).

All these conclusions require several cautionary notes that highlight a roadmap for future research. First, the number of records per species is generally low, and temnocephalid records are disproportionately concentrated in the northwestern parts of the Dinaric Karst (Fig. 2), which most likely reflects sampling bias. Given the limited data, we could not correct this bias using rarefaction. More intensive and spatially balanced sampling could therefore alter the observed patterns and potentially reveal stronger host or site specificity. Second, although we found no association between temnocephalid species and recent cave shrimp lineages, the hypothesis of coevolution should not be dismissed before molecular revision of temnocephalids. Cryptic species are a relatively ubiquitous phenomenon in nature (Eme et al. 2018; Li and Wiens 2023), and it seems unlikely that such small flatworms, lacking many visible diagnostic traits, are genetically homogenous entities along the Dinaric Karst where their hosts are highly genetically structured (Zakšek et al. 2009). We cannot rule out that at least some populations might, in fact, be genetically distinct, and that temnocephalids coevolved with their hosts. Noteworthy, two species of temnocephalids were also described from cave shrimps (currently genus *Xiphocaridinella*), in one cave on the Caucasus (Joffe and Djanashvili 1981) and, therefore, represent an interesting venue to explore the coevolution with their host, as there was a relatively young connection between the Dinaric Karst and the Caucasus as revealed from cave shrimp phylogeny (Zakšek et al. 2007). Finally, note that the potentially unresolved taxonomic status of temnocephalid species does not necessarily refute our conclusions: temnocephalids may still be host-nonspecific and mobile on a local scale. In this case, low co-occurrences do not indicate competitive interactions, but rather spatial segregation around their host populations. This is also the third potential caveat in our interpretation of the data, which is suffering from a comparative approach. Rectifying this issue requires an experimental study of temnocephalid host choice, host body part and movement capacity (see challenges associated with experiments on subterranean organisms (Mammola et al. 2021)).

Overall, all conclusions should be considered as working hypotheses, paving the way for future studies. A better understanding of epizoic interactions will require molecular delimitation of temnocephalid species, reconstruction of their phylogenetic relationships and improved spatial resolution of temnocephalid distributions.

Authors contributions

C.F. collected the data. C.F. and V.Z. jointly conceived the study. E.P. performed the data analysis. E.P. and V.Z. prepared figures. C.F. wrote the first draft. All authors reviewed and edited the full manuscript before submission.

Data availability

The data and scripts used are available in Zenodo at https://doi.org/10.5281/zenodo.18355834.

Acknowledgements

We thank Maja Kajin for her advisory role in statistics and Teo Delić for providing photographs used in Fig. 1. The study was funded by the Slovenian Agency for Research and Innovation through the core program P1-0184 and PhD funding to EP. The study was additionally supported by **Biodiversa+**, the European Biodiversity Partnership under the 2021–2022 BiodivProtect joint call for research proposals in the context of DarCo, co-funded by the European Commission (GA N°101052342) and with the funding organisations Ministry of Universities and Research (Italy), Agencia Estatal de Investigación – Fundación Biodiversidad (Spain), Fundo Regional para a Ciência e Tecnologia (Portugal), Suomen Akatemia – Ministry of the Environment (Finland), Belgian Science Policy Office (Belgium), Agence Nationale de la Recherche (France), Deutsche Forschungsgemeinschaft e.V. – BMBF-VDI/VDE INNOVATION + TECHNIK GMBH (Germany), Schweizerischer Nationalfonds zur Forderung der Wissenschaftlichen Forschung (Switzerland), Fonds zur Förderung der Wissenschaftlichen Forschung (Austria), Ministry of Higher Education, Science and Innovation (Slovenia), and the Executive Agency for Higher Education, Research, Development and Innovation Funding (Romania); and **Biodiversa+**, the European Biodiversity Partnership, in the context of the Sub-BioMon - Developing and testing approaches to monitor subterranean biodiversity in karst project under the 2022–2023 BiodivMon joint call. It was co-funded by the European Commission (GA N°101052342) and the following funding organisations: Ministry of Higher Education, Science and Innovation (Slovenia), The Belgian Science Policy (Belgium), Ministry of Universities and Research (Italy), National Research, Development and Innovation Office (Hungary), Executive Agency for Higher Education, Research, Development and Innovation Funding (Romania). Part of the equipment used in this study was purchased for the project "Development of research infrastructure for the international competitiveness of the Slovenian **RRI space –RI-SI-LifeWatch**". The operation is co-financed by the Republic of Slovenia, Ministry of Education, Science and Sport and the European Union from the European Regional Development Fund.

References

Almeida-Neto M, Guimarães P, Guimarães PR, Loyola RD, Ulrich W (2008) A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos 117: 1227–1239. https://doi.org/10.1111/j.0030-1299.2008.16644.x

Amin OM, Heckmann RA, Fišer Ž, Zakšek V, Herlyn H, Kostanjšek R (2019) (Acanthocephala: Echinorhynchidae) from *Proteus anguinus* Laurenti (Amphibia: Proteidae) and the cave ecomorph of *Asellus aquaticus* (Crustacea: Asellidae) in Slovenia. Folia Parasitologica 66. https://doi.org/10.14411/fp.2019.015

Benko G, Kostanjšek R, Fišer Ž (2024) Behavioural alterations in surface and cave populations of isopod crustacean *Asellus aquaticus* by *Acanthocephalus anguillae*. Journal of Helminthology 98: e84. https://doi.org/10.1017/S0022149X24000592

Blair D, Cannon LRG, Littlewood DTJ, Olson PD, Sewell KB (2023) The Temnocephalidae (Platyhelminthes): molecular data illuminate the evolution of an ancient group of symbiotic flatworms. Systematics and Biodiversity 21: 2174611. https://doi.org/10.1080/14772000.2023.2174611

Brodersen J, Post DM, Seehausen O (2018) Upward Adaptive Radiation Cascades: Predator Diversification Induced by Prey Diversification. Trends in Ecology & Evolution 33: 59–70. https://doi.org/10.1016/j.tree.2017.09.016

Cardoso P, Mammola S, Rigal F, Hilario R, Carvalho J (2024) BAT: Biodiversity Assessment Tools. CRAN: Contributed Packages. https://doi.org/10.32614/CRAN.package.BAT

Chesson P (2000) Mechanisms of Maintenance of Species Diversity. Annual Review of Ecology and Systematics 31: 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Delić T, Trontelj P, Zakšek V, Fišer C (2016) Biotic and abiotic determinants of appendage length evolution in a cave amphipod. Journal of Zoology 299: 42–50. https://doi.org/10.1111/jzo.12318

Delić T, Di Batista Borko Š, Premate E, Rexhepi B, Alther R, Knüsel M, Malard F, Weber D, Stoch F, Flot J-F, Fišer C, Altermatt F (2025) Phylogenetic origin of morphologically cryptic species shapes co-occurrence and sympatry patterns. Freshwater Biology 70: e70000. https://doi.org/10.1111/fwb.70000

Dormann CF, Frund J, Bluthgen N, Gruber B (2009) Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks. The Open Ecology Journal 2: 7–24. https://doi.org/10.2174/1874213000902010007

Eme D, Zagmajster M, Delić T, Fišer C, Flot J-F, Konecny-Dupré L, Palsson S, Stoch F, Zakšek V, Douady CJ, Malard F (2018) Do cryptic species matter in macroecology? Sequencing European groundwater crustaceans yields smaller ranges but does not challenge biodiversity determinants. Ecography 41: 424–436. https://doi.org/10.1111/ecog.02683

Fišer C, Luštrik R, Sarbu SM, Flot J-F, Trontelj P (2015a) Morphological Evolution of Coexisting Amphipod Species Pairs from Sulfidic Caves Suggests Competitive Interactions and Character Displacement, but No Environmental Filtering and Convergence. PLoS ONE 10: e0123535. https://doi.org/10.1371/journal.pone.0123535

Fišer C, Delić T, Luštrik R, Zagmajster M, Altermatt F (2019) Niches within a niche: ecological differentiation of subterranean amphipods across Europe's interstitial waters. Ecography 42: 1212–1223. https://doi.org/10.1111/ecog.03983

Fišer Ž, Altermatt F, Zakšek V, Knapič T, Fišer C (2015b) Morphologically cryptic amphipod species sre "ecological clones" at regional but not at local scale: a case study of four *Niphargus* species. PLoS ONE 10: e0134384. https://doi.org/10.1371/journal.pone.0134384

Fišer C, Premate E (2024) Phenotype Variation in *Niphargus* (Amphipoda: Niphargidae): Possible Explanations and Open Challenges. Diversity 16(7): 375. https://doi.org/10.3390/d16070375

Gelder SR (1999) Zoogeography of branchiobdellidans (Annelida) and temnocephalidans (Platyhelminthes) ectosymbiotic on freshwater crustaceans, and their reactions to one another in vitro. Hydrobiologia 406: 21–31. https://doi.org/10.1023/A:1003755630718

Gibert J, Deharveng L (2002) Subterranean Ecosystems: A Truncated Functional Biodiversity. BioScience 52: 473–481. https://doi.org/10.1641/0006-3568(2002)052[0473:SEATFB]2.0.CO;2

Griffith DM, Veech JA, Marsh CJ (2016) cooccur: Probabilistic Species Co-Occurrence Analysis in R. Journal of Statistical Software 69: 1–17. https://doi.org/10.18637/jss.v069.c02

Hutchins BT, Schwartz BF, Nowlin WH (2014) Morphological and trophic specialization in a subterranean amphipod assemblage. Freshwater Biology 59: 2447–2461. https://doi.org/10.1111/fwb.12440

Joffe BI, Djanashvili RA (1981) The first record of temnocephalids in the territory of the USSR. Parazitologiya 15: 170–174.

Jugovic J, Prevorčnik S, Aljančič G, Sket B (2010) The atyid shrimp (Crustacea: Decapoda: Atyidae) rostrum: phylogeny versus adaptation, taxonomy versus trophic ecology. Journal of Natural History 44: 2509–2533. https://doi.org/10.1080/00222933.2010.502258

Jugovic J, Fišer C, Delić T, Zagmajster M, Zakšek V (2026) Revealing European cave shrimp diversity: a new species of *Spelaeocaris* (Decapoda, Atyidae) named through public participation. Zookeys 1267: 51–76. https://doi.org/10.3897/zookeys.1267.176622

Leibold MA, McPeek MA (2006) Coexistence of the niche and neutral perspectives in community ecology. Ecology 87: 1399–410. https://doi.org/10.1890/0012-9658(2006)87[1399:cotnan]2.0.co;2

Li X, Wiens JJ (2023) Estimating Global Biodiversity: the Role of Cryptic Insect Species. Systematic Biology 72: 391–403. https://doi.org/10.1093/sysbio/syac069

Mammola S (2019) Finding answers in the dark: caves as models in ecology fifty years after Poulson and White. Ecography 42: 1331–1351. https://doi.org/10.1111/ecog.03905

Mammola S, Isaia M (2014) Niche differentiation in *Meta bourneti* and *M. menardi* (Araneae, Tetragnathidae) with notes on the life history. International Journal of Speleology 43: 343–353. https://doi.org/10.5038/1827-806x.43.3.11

Mammola S, Arnedo MA, Fišer C, Cardoso P, Dejanaz AJ, Isaia M (2020) Environmental filtering and convergent evolution determine the ecological specialization of subterranean spiders. Functional Ecology 34. https://doi.org/10.1111/1365-2435.13527

Mammola S, Lunghi E, Bilandžija H, Cardoso P, Grimm V, Schmidt SI, Hesselberg T, Martinez A (2021) Collecting eco-evolutionary data in the dark: Impediments to subterranean research and how to overcome them. Ecology and Evolution 11: 5911–5926. https://doi.org/10.1002/ece3.7556

Matjašič J (1956) Opazovanja na jamskem suktoriju *Spelaeophrya troglocaridis* Stammer. Biološki vestnik 5: 71–73.

Matjašič J (1990) Monography of the family Scutariellidae (Turbellaria, Temnocephalidea) = Monografija družine Scutariellidae (Turbellaria, Temnocephalidea). Slovenska akademija znanosti in umetnosti, Ljubljana.

Medina M, Baker DM, Baltrus DA, Bennett GM, Cardini U, Correa AMS, Degnan SM, Christa G, Kim E, Li J, Nash DR, Marzinelli E, Nishiguchi M, Prada C, Roth M, Saha M, Smith CI, Theis KR, Zaneveld J (2022) Grand Challenges in Coevolution. Frontiers in Ecology and Evolution 9: 618251. https://doi.org/10.3389/fevo.2021.618251

Pavlek M, Mammola S (2020) Niche-based processes explaining the distributions of closely related subterranean spiders. Journal of Biogeography: 1–16. https://doi.org/10.1111/jbi.13987

Premate E, Fišer C (2024) Functional trait dataset of European groundwater Amphipoda: Niphargidae and Typhlogammaridae. Scientific Data 11: 188. https:/doi.org/10.1038/s41597-024-03020-w

Premate E, Zagmajster M, Fišer C (2021a) Inferring predator–prey interaction in the subterranean environment: a case study from Dinaric caves. Scientific Reports 11: 1–9. https://doi.org/10.1038/s41598-021-01249-8

Premate E, Borko Š, Delić T, Malard F, Simon L, Fišer C (2021b) Cave amphipods reveal co-variation between morphology and trophic niche in a low-productivity environment. Freshwater Biology 66: 1876–1888. https://doi.org/10.1111/fwb.13797

R Development Core Team (2024) A language and environment for statistical computing. https://doi.org/10.32614/r.manuals

Schluter D (2000) Ecological Character Displacement in Adaptive Radiation. The American Naturalist 156: S4–S16. https://doi.org/10.1086/303412

Stuart YE, Losos JB (2013) Ecological character displacement: glass half full or half empty? Trends in Ecology & Evolution 28: 402–408. https://doi.org/10.1016/j.tree.2013.02.014

Trontelj P, Blejec A, Fišer C (2012) Ecomorphological Convergence of Cave Communities. Evolution 66: 3852–3865. https://doi.org/10.1111/j.1558-5646.2012.01734.x

Veech JA (2013) A probabilistic model for analysing species co-occurrence. Global Ecology and Biogeography 22: 252–260. https://doi.org/10.1111/j.1466-8238.2012.00789.x

Vellend M (2010) Conceptual synthesis in community ecology. The Quarterly review of biology 85: 183–206. https://doi.org/10.1086/652373

Weigand AM, Kremers J, Grabner DS (2016) Shared microsporidian profiles between an obligate (*Niphargus*) and facultative subterranean amphipod population (*Gammarus*) at sympatry provide indications for underground transmission pathways. Limnologica 58: 7–10. https://doi.org/10.1016/j.limno.2016.01.005

Zakšek V, Sket B, Trontelj P (2007) Phylogeny of the cave shrimp *Troglocaris*: Evidence of a young connection between Balkans and Caucasus. Molecular Phylogenetics and Evolution 42: 223–235. https://doi.org/10.1016/j.ympev.2006.07.009

Zakšek V, Sket B, Gottstein S, Franjević D, Trontelj P (2009) The limits of cryptic diversity in groundwater: Phylogeography of the cave shrimp *Troglocaris anophthalmus* (Crustacea: Decapoda: Atyidae). Molecular Ecology 18: 931–946. https://doi.org/10.1111/j.1365-294X.2008.04061.x